Sea lamprey (*Petromyzon marinus*) transit of a ramp equipped with studded substrate: implications for fish passage and invasive species control

John B. Hume[1] †, Martyn C. Lucas[2], Ulrich Reinhardt[3], Peter J. Hrodey[4], and C. Michael Wagner[1]

Final accepted version as published in *Ecological Engineering* **155**, xxx-xxx. Accepted 19 June 2020, Published 29 June 2020. DOI: 10.1016/j.ecoleng.2020.105957

[1] *Rm 13, Natural Resources Building, 480 Wilson Road, Fisheries & Wildlife Department, Michigan State University, East Lansing, MI 48824,* jhume@msu.edu, mwagner@msu.edu; [2] *Department of Biosciences, University of Durham, South Road, Durham, England, United Kingdom DH1 3LE*, m.c.lucas@durham.ac.uk; [3] *Eastern Michigan University, Biology Department, 403A Mark Jefferson Science Complex, Ypsilanti, MI 48197*, ureinhard@emich.edu; [4] *U.S. Fish & Wildlife Service, Marquette Biological Station, 3090 Wright St, Marquette, MI 49855*, pete_hrodey@fws.gov.

† Corresponding author. Tel. 517-353-5485.

ABSTRACT

1. Anguilliform-swimming fishes (eels, lampreys) are undergoing large and global declines due partly to an inability to pass dams via traditional fishways. The installation of "eel ladders" (wetted, studded/bristle substrates that permit these fishes to climb over obstructions) offer a potential solution.

2. We examined the behaviour of migrating sub-adult sea lamprey (*Petromyzon marinus*) as they approached and attempted to ascend a 45° studded ramp in a mesocosm placed in a river. We also examined motivation to use the ramp in the presence of a conspecific alarm cue that signals predation risk.

3. Entrance (75%) and attraction efficiency (85%) were high, but reduced by the presence of alarm cue. In total, 98% of sea lamprey attracted to the base of the ramp ascended, and alarm cue had no effect. Time to ascend the ramp (post-release) was variable (1 – 521 min) and on average was 119 min (50% probability = 35 min). Few sea lamprey required multiple attempts to ascend (19.8%) and was more likely during longer transit times, with multiple ramp attachments, and with higher body mass. Propensity to attach to the ramp increased with number of attempts. The high efficacy of this design, compared to poor-mediocre efficiencies of similar designs in previous studies, may be related to water velocity and depth, geometry of substrate studs, substrate presentation (horizontal/vertical, and incline), and length of studded substrate.

4. Studded ramps represent a substantial opportunity for managers attempting to selectively pass anguilliform fishes over dams, aiding conservation efforts. Applications to the management of sea lamprey include removal in their non-native Great Lakes range, and fish passage in their native range.

INTRODUCTION

Diadromous fishes have experienced drastic declines in the last 300 years, and many have been extirpated at least in part due to river channel disconnection by anthropogenic barriers (Limburg and Waldman 2009; Birnie-Gauvin et al. 2018). Designed for the acquisition of energy, storage of water, and protection from floods, the rate of barrier construction is high and will likely continue to increase globally (Grill et al. 2015) despite recognized negative effects on aquatic ecology (Nilsson et al. 2005; Poff and Zimmerman 2010). Blockage of migration routes and habitat fragmentation due to the presence of barriers, poses a threat to the persistence of fishes that require freshwater habitats to complete their life cycle (Lucas and Baras 2001). Migratory fishes can be physically isolated from critical habitats or have their access to it restricted (Pringle 2003; Radinger and Wolter 2014; Lynch et al. 2016). As a consequence, there is increased focus on restoring habitat connectivity for migratory fishes through barrier removal (Poff and Hart 2002) and the construction of engineered fish passage devices (= "fishways", Tummers et al. 2016a; Silva et al. 2018). Fishways do not appear to be a consistently effective mitigation tool, however, and although the reasons for their inefficiency can be obscure, it likely stems from a lack of biological knowledge of the target species leading to inappropriate fishway design (Kemp 2016; Silva et al. 2018).

Migratory fishes exhibit swimming capacities and behaviours that evolved in response to challenges faced over long geological time scales. Consequently, the tendencies and abilities of these fishes today are in effect constrained by historical processes. The efficiency of technical fishways is variable and generally low-moderate for many fishes (Bunt et al. 2012), suggesting they have limited utility in restoring populations. These highly engineered structures often generate a mismatch between the evolved set of abilities of migratory fishes and the "task" we impose on them when attempting to bypass barriers. Fishways that exploit species-specific abilities should conceivably operate more effectively than those that do not. In recent decades, there has been an increased shift towards rendering fishways "transparent" by explicitly considering animal behaviour during fishway approach and passage attempts (Castro-Santos and Haro 2010). This has led to an increase in nature-like bypasses, which can be more effective than technical fishways (Bunt et al. 2012) but not always (Aarestrup et al. 2003). Despite increasing focus on the needs of other species impacted by barriers, fish passage research, at least in the northern hemisphere, remains firmly rooted in salmonid biology despite substantial differences among migratory taxa

(Birnie-Gauvin et al. 2018). Fishes with anguilliform swimming modes (e.g. eels, *Anguilla* spp. and lampreys, Petromyzontiformes) are not widely benefitting from fishways. Anguilliform fishes have a low propeller efficiency relative to salmonids, but they are highly efficient long-distance swimmers (Beamish 1974; McCleave 1980; van Ginneken et al. 2005) with a tendency to utilize low-velocity boundary layers in rivers created by hydraulically-rough stream beds (e.g. Jellyman 1977; Reid and Goodman 2016). Furthermore, their morphology suggests that anguilliform-specific fishway designs (e.g. Solomon and Beach 2004) could better exploit these characteristics to realize higher rates of anguilliform passage.

Passing anguilliform fishes over barriers by using plastic substrates bearing bristles or pegs ("eel ladders" or "studded tiles") is an increasingly common management approach, and one capable of realizing high rates of upstream passage for some species (e.g. European eel *Anguilla anguilla,* Vowles et al. 2015, 2017). Lamprey-specific fishway designs have realised vast improvements in passage rates of Pacific lamprey *Entosphenus tridentatus* over conventional fishways in western North America, based on inclined or even vertical surfaces permitting attachment during ascent (Moser et al. 2015; Goodman and Reid 2017). For other species such as European river lamprey *Lampetra fluviatilis* several fishway designs may act as *de facto* barriers (Laine et al. 1998; Foulds and Lucas 2013). For this species, addition of studded or bristle substrate has been shown to modestly improve ascent, with passage success efficiencies of 7 - 37% reported for several laboratory and field conditions (Kerr et al. 2015; Vowles et al. 2017; Tummers et al. 2016b, 2018). In Ireland, only 8% of available anadromous sea lamprey (*Petromyzon marinus*) passed sloping weirs modified with studded tile sections (Rooney et al. 2015). Therefore, there are aspects of lamprey interaction with inclined studded surfaces we do not yet fully understand and which certainly go beyond swimming capacity alone (Kirk and Caudill 2017; Castro-Santos et al. 2017; Goodman and Reid 2017). Resolving these uncertainties, be they mechanical, physiological, or behavioural in nature, is key to designing effective fishways for a range of management scenarios but is rarely attempted.

The sea lamprey is both imperiled in parts of its native range (eastern North America and Europe) and a devastating invasive species in the Laurentian Great Lakes (Hansen et al. 2016). The greatest threat to their restoration in native ranges - the presence of barriers limiting access to spawning habitat (Maitland et al. 2015; Docker and Hume 2019) - is also a principal means by which invasive populations are kept under control (McLaughlin et al. 2007). But these barriers present significant obstacles to non-target fishes that, like sea lamprey, cannot pass over the barrier lip (Porto et al. 1999; Dodd et al. 2003). Therefore, identifying a means to permit passage of non-target species while preventing sea lamprey from doing so is a major priority in the Great Lakes (McLaughlin et al. 2003). Prior attempts to achieve "selective fragmentation" (Rahel and McLaughlin 2018) in the Great Lakes using strictly physical means have thus far exhibited limited success (Klingler et al. 2003; Lavis et al. 2003; McLaughlin et al. 2007; Pratt et al. 2009). Behaviour manipulation using a repellent conspecific odor (an alarm cue released from damaged tissues) is a promising new approach that could reduce sea lamprey passage opportunities in the

Great Lakes. By eliciting an aversive reaction to the perception of predation risk, the alarm cue can redistribute sub-adult sea lamprey within streams during the spawning migration (Wagner et al. 2011; Hume et al. 2015; Luhring et al. 2016). Therefore, the alarm cue may prevent sea lamprey from entering fishways designed for other species while pushing them towards a trap. Alternatively, to aid conservation in their native range the alarm cue could operate in a similar fashion by improving encounter rates with fishway entrances (Byford et al. 2016). Furthermore, their anguilliform shape and propensity to attach to surfaces while resting enables lampreys to ascend inclined surfaces, suggesting ramps bearing narrowly-spaced studs could be a unique manner of selectively removing sea lamprey from Great Lakes streams (D'Aguiar 2011), or improving passage over barriers in their native range.

The goal of this study was to test an existing studded substrate design ("eel ladder", Milieu Inc.) for passing anguilliform fishes over barriers, and assess its potential for use in sea lamprey management using a variety of behavioural metrics. We constructed a large, in-stream mesocosm containing a ramp at the upstream end that was fitted with studded plastic substrate. We then tested this design with actively migrating sea lamprey collected from tributaries to the Laurentian Great Lakes, situating the mesocosm within a stream that naturally attracts sea lamprey searching for spawning habitat each spring-summer. Our primary objectives were *i*) to test sea lamprey transit efficiency of a ramp extending from the surface of the stream, and *ii*) establish the effect of alarm cue on sea lamprey motivation to interact with and ascend the ramp.

MATERIALS & METHODS

Apparatus

We conducted trials in the Ocqueoc River, Michigan, U.S.A., immediately upstream of a fixed-crest sea lamprey barrier (45°28'50.7" N, 84°06'36.3" W) during June-July 2016. We constructed a 6 x 1 x 1 m channel from 1.9 cm thick PVC panels (U.S. Plastic Corp.) and fitted it with a 45° angled ramp that was 2.38 x 0.42 m long, forming a head of 1.8 m (Fig. 1). A 30° angled chute extended from the crest of the ramp to provide a less severe transition for any ascending sea lamprey and direct them into a box trap positioned behind the ramp. Transition zones are key areas of failure to ascend inclined surfaces in other lamprey species (e.g. Frick et al. 2017). Water depth within the stream was 0.69 m, resulting in 1.59 m of the ramp extending above the surface. The ramp was fitted with a substrate comprised of horizontally-mounted 2 mm thick ABS plastic studs 11.4 cm tall with a minimum diagonal distance between pegs of 3 cm (Milieu Inc., Canada; Fig. 2a). We supplied stream water to the ramp using 2 x 4000 gallon per hour Alpine Cyclone Pumps via a spray bar mounted at the crest, producing a flow rate of 0.6 L s^{-1}. Depth of water between studs on the exposed section of the ramp was 69.2 ± 1.66 mm, and velocity was estimated at 0.2 m s^{-1} between studs. Adjacent to the ramp within the channel, flow was permitted from the stream

through a mesh screen, excluding sea lamprey from moving behind the ramp and providing attraction flow at 0.12 m^3 s^{-1}.

Extending from the entrance to the channel was a 10 x 1 x 1.23 m enclosure made from #126 white knotless netting (1.27 cm square mesh, Memphis Net and Twine). We secured the base of this arena with sandbags and the top of the nets suspended from floats and fastened to posts driven into the stream bed to prevent escape of sea lamprey. The apparatus was telemetered with four passive integrated transponder (PIT) antennas wired to a single multiplexer (Oregon RFID Inc.) that recorded date, time, and location of tagged sea lamprey released from holding cages positioned at the most downstream extent of the arena. We positioned a full-width antenna across the arena 2 m upstream of the holding cages to detect sea lamprey upon their release at the beginning of a trial (A1); a second antenna (A2) was fitted in a loop around the entrance to the PVC channel, 10 m upstream from the holding cages, to detect sea lamprey that moved up and entered the channel; and we positioned a third antenna (A3) at the base of the ramp, to detect sea lamprey that approached. We fitted a final antenna (A4) 1.6 m from the base of the ramp, to detect sea lamprey that made an attempt to ascend. The full extent of the exposed ramp section was illuminated by an infrared floodlight (CMVision IR110 - 114 LED Indoor/Outdoor Long Range 200-250ft IR Illuminator) and monitored by an IR-sensitive camera (960H Security DVR Surveillance System, single Bullet Infrared, CCTV Camera Pros) to record sea lamprey attempting to ascend (Fig. 3; Supplementary video files).

Experimental Design

Sea lamprey migrating upstream to spawn in tributaries of Lakes Michigan and Huron were captured in traps and provided by the U.S. Fish and Wildlife Service (USFWS) Sea Lamprey Control Program during routine assessment operations. They were subsequently transported to and maintained at the U.S. Geological Survey's (USGS) Hammond Bay Biological Station, Millersburg, Michigan, U.S.A. within 1000 L capacity holding tanks, each supplied with Lake Huron water at ambient temperatures (5 - 18°C). Sea lamprey we selected for inclusion in trials were weighed (g) and measured (mm, TL) before being uniquely marked with 32 mm PIT tags surgically inserted into the body cavity. We used three hundred female sea lamprey in trials, with a mean wet weight of 227 g (range = 95 – 390 g) and mean length of 469 mm (range = 323 – 571 mm). Only female sea lamprey were used in trials because the location of the experiment was upstream of a barrier designed to prevent sea lamprey access to spawning habitat, so there was a need to minimize the risk of escapement and subsequent spawning success. All handling and tagging procedures were conducted in accordance with Michigan State University Institutional Animal Care and Use Committee permit #02/16-017-00.

We conducted 30 trials total (one per night), 15 with and 15 without (control) the presence of a sea lamprey alarm cue that was prepared per the methodology described in Bals and Wagner

(2012). Two hours prior to each trial beginning, we estimated discharge (m^3 s^{-1}) at the midpoint of the PVC channel entrance by using the USGS midsection method (Gore 1996) with a Doppler flow meter (Flo-Mate Model 2000, Marsh-McBirney). During alarm cue treatments this estimate enabled calculation of alarm cue volume necessary to produce a concentration of 1 ppm when combined with half of the PVC channel's discharge. We introduced alarm cue by mixing the extract with stream water and delivered directly to a point adjacent to the base of the ramp (rate = 60 mL h^{-1} for 4 h, 2200 – 0200 hours) using a peristaltic pump (Masterflex 7553-70, Cole-Parmer) powered by a 12 V battery. We determined the point source of alarm cue using dye releases (Rhodamine WT), where only one-half of the PVC channel would contain the alarm cue for the furthest possible extent. However, it was not possible to produce a clean separation given the channel's narrow width and turbulent flow, thus full mixing occurred at the entrance. Sea lamprey are primarily nocturnal at this stage in their life cycle and so we began trials at sunset. For each trial we placed 10 sea lamprey in a holding cage at the downstream extent of the arena 2 hours prior to release at 2200 hrs. We then released sea lamprey and left them undisturbed to explore the arena and interact with the channel and ramp. The following morning we removed any sea lamprey that ascended the ramp from the box trap, counted them, and re-identified individuals. We then transferred telemetry and video data daily onto external media and prepared it for analysis.

Analysis

We considered only detections during the first 24 hours post-release for analysis and examined multiple metrics of sea lamprey interaction with the ramp to evaluate ramp performance and sea lamprey behaviour (Table 1). Firstly, we defined attraction efficiency of the ramp as the percent of sea lamprey detected on A3 (base of ramp) that were previously detected on A2 (entrance to channel). We calculated transit efficiency based on the percent of sea lamprey removed from the box trap that were previously detected on A3 (base of ramp). We used chi-square tests to compare observed *vs* expected values for attraction efficiency and transit efficiency between treatments. Additionally, we used a generalized linear model (GLM) with Poisson regression to examine factors explaining the observed transit efficiency. We tested for multicollinearity of factors using Collinearity Tolerance and Variance Inflation Factors, with a threshold of > 0.2 and < 10, respectively and removed any with high intercorrelations. We ran a main-effects model and all 2-way interactions of delay, treatment, number of transit attempts, number of attachments, mesocosm channel discharge, water temperature, body length, and body weight. We fitted a multinomial logistic regression to the data to quantify the effect of parameters on the number of transit attempts. These parameters included: position at ramp entrance, treatment, delay, frequency of detections on A3, number of attachments, discharge, temperature, body length, and body weight. Position at the ramp entrance was determined visually from video files by dividing the ramp base into three equal sections. (left, center, right). We used the same multinomial logistic regression approach to examine those factors influencing the number of attachments, where the number of transit attempts was substituted in. Finally, we plotted the cumulative probability of sea lamprey

moving upstream, entering the PVC channel, approaching the ramp, and ascending the ramp in either treatment, and analysed transit probability using a Kaplan-Meier product-limit estimator and Mantel-Cox statistic, which provides the probability for an event (transit, or failure to transit). Analyses were conducted in IBM SPSS Statistics (v.24).

RESULTS

All sea lamprey were detected moving in an upstream direction through the mesocosm following their release (100%, $n = 300$). Of these, a total of 225 subsequently entered the channel containing the ramp (75%). Alarm cue treatment did not statistically significantly affect the number of sea lamprey that entered the channel following their release (Pearson's chi-square, $\chi^2 = 0.992$, d.f. = 1, $P = 0.32$). However, more individuals were detected entering the channel on nights without alarm cue compared to when it was present ($n = 132/150$ *vs* $n = 93/150$; Fig. 4). Total attraction efficiency to the ramp itself was 85.3% ($n = 192/225$) and although alarm cue had no statistically significant effect ($\chi^2 = 3.3313$, d.f. = 1, $P = 0.068$) once again more individual sea lamprey were detected at the base of the ramp on nights when alarm cue was absent ($n = 127$ *vs* $n = 65$; Fig. 4).

Total transit efficiency of the ramp was high (97.9%, $n = 188/192$) and was significantly influenced by treatment ($\chi^2 = 6.1311$, d.f. = 1, $P = 0.013$). On nights when alarm cue was present within the channel fewer sea lamprey ascended the ramp ($n = 63$) compared to nights when it was absent ($n = 125$). However, when considering treatments separately, transit efficiency was almost exactly the same (control = 98.4%, alarm cue = 96.9%; Fig. 4). A GLM revealed two factors had significant effects on transit efficiency, treatment ($W = 7.151$, $P = 0.007$) and number of transit attempts ($W = 9.549$, $P = 0.002$). The presence of alarm cue within the channel reduced the likelihood of sea lamprey transiting the ramp, and transit was more likely with an increasing number of attempts. A significant interaction term was also revealed, treatment*discharge where a higher discharge from the channel reduced the likelihood of transit either in the presence of alarm cue ($W = 4.028$, $P = 0.045$) or not ($W = 5.875$, $P = 0.015$).

Delay was not a significant factor predicting transit efficiency, with sea lamprey that did ascend the ramp doing so in 119 min on average (range = 1 – 503 min) and those that failed to do so delayed an average of 127 min before moving downstream (range = 1 – 521 min) (Fig. 5). Treatment also had no significant effect on delay (Mantel-Cox test = 0.081, d.f. = 1, $P = 0.776$). In the presence of alarm cue transit was only marginally slower compared to when it was absent (50% probability of transit = 35 min *vs* 34 min). However, treatment was a significant factor explaining the time to last detection within the arena among those sea lamprey that failed to ascend the ramp (Mantel-Cox test = 4.703, d.f. = 1, $P = 0.03$). When alarm cue was present within the channel sea lamprey ceased moving earlier compared to when alarm cue was absent (50% probability of last detection = 52 min *vs* 232 min).

In total, of 192 sea lamprey that made at least one attempt to ascend the ramp only four failed to do so successfully (2.1%). Of those attempting, 37 (19.8%) made more than a single attempt, up to a maximum of nine separate attempts. Multinomial logistic regression revealed three factors significantly influencing the number of attempts to ascend, delay ($P < 0.001$), number of attachments ($P < 0.001$), and body weight ($P = 0.004$). Sea lamprey were more likely to make more than a single attempt to ascend the ramp if they experienced a longer delay prior to their first attempt, attached more frequently to the ramp surface during ascent, or had a larger body mass. Of the 192 individual sea lamprey that made at least one attempt to ascend the ramp 29.2% ($n = 56$) attached to the surface. Three factors significantly influenced this behaviour, number of transit attempts ($P < 0.001$), frequency of detections at the base of the ramp ($P = 0.005$), and position at ramp entrance ($P = 0.042$). Sea lamprey that made more than one attempt to ascend, were detected more frequently at the base of the ramp prior to making an attempt, and those beginning their ascent within the central third of the ramp had a greater likelihood of attaching to the ramp surface during transit.

DISCUSSION

Bypassing barriers to aid fish migration using conventional fishways has variable (often poor or mediocre) effectiveness for non-salmonid species (Bunt et al. 2012; Sanz-Ronda et al. 2017; Silva et al. 2018). Despite recent deployment of anguilliform-specific fishways, their efficiency and the mechanisms underpinning that efficiency, remain poorly understood compared to "salmo-centric" designs (Watz et al. 2019). Here, we quantified the performance of a ramp bearing a studded plastic substrate that could facilitate the transit of sea lamprey over a barrier; an event that may culminate in either their capture (i.e. to improve invasive species control), or passage (i.e. to aid restoration). This design exhibited both high rates of attraction to (85%) and subsequent ascent of the ramp (98%). In addition, we found that the presence of a repellent, species-specific semiochemical (sea lamprey alarm cue, Wagner et al. 2011) can influence the outcome by reducing attraction efficiency. Although we interpret these findings conservatively in light of the experimental circumstances (constrained movement opportunities for test lamprey), they do represent considerable improvements on rates of passage for sea lamprey at sloping weirs with sections of studded substrate (Rooney et al. 2015). Studded ramps such as that tested here could also represent an opportunity to selectively remove sea lamprey from Great Lakes tributaries and aid desirable fish passage (D'Aguiar 2011; Rahel and McLaughlin 2018).

All tagged sea lamprey in this study moved upstream within the mesocosm following release, indicating little to no effect of handling or tag insertion on their typical upstream-oriented movement during this life stage. Total entrance efficiency into the PVC channel containing the ramp was 75%, which is high compared to the average percent entrance reported for anadromous sea lamprey entering four fishways in the Connecticut River (4 – 64%, Castro-Santos et al. 2017). Castro-Santos et al. (2017) suggest the transition from natural to engineered environments may be

difficult for anadromous sea lamprey, resulting in low entrance rates observed at fishways in large dams. Although exact mechanisms remain obscure, individual sea lamprey may exhibit an aversion for certain materials within fishways if they fail to achieve sufficient suction (Adams and Reinhardt 2008), resulting in failure to enter, or fall back following entrance. The majority of sea lamprey in this study successfully entered a channel fashioned from smooth PVC plastic and approached the ramp. High attraction efficiency to the ramp (85.3% total) could be attributed to the turbulence generated by water cascading down the ramp itself. This would support Kirk et al. (2017) who reported Pacific lamprey were attracted to turbulent areas in low-flow fishway environments. In nature, this response would enable migratory lampreys to locate potential routes past obstacles by indicating a secondary source of water that could be exploited using their suctorial discs, either via climbing (Kemp et al. 2009) or burst-swim-and-attach movements (Quintella et al. 2004).

Our study revealed a 16% reduction in entrance efficiency in the presence of alarm cue (132/150 control *vs* 93/150 alarm cue), but alarm cue did not prevent entrance into the PVC channel. This is consistent with applications of this odor in natural environments, where its presence does not prevent sea lamprey from migrating upstream or entering tributaries containing the odor but does induce various predator avoidance behaviours including spatial avoidance (Hume et al. 2015; Luhring et al. 2016). This odor is hypothesized to indicate areas of risk caused by injury or predation to conspecifics (Imre et al. 2010; Wagner et al. 2011) and may therefore result in a lowered likelihood of sea lamprey undertaking risky behaviour in its presence (e.g. entering an engineered structure *vs* holding in stream). There are consistent individual differences (CIDs) between sub-adult sea lamprey in behaviour that may influence interactions with novel environments such as fishway entrances or traps. Sea lamprey recovered from a trap exhibit higher general activity levels than at-large individuals, and respond to a putative predator cue by decreasing their activity whereas at-large sea lamprey do not (McLean and McLaughlin 2018). These CIDs (exploration, activity, and risk-taking) are factors that likely alter the probability of sea lamprey encountering and then entering fishway entrances. Reinhardt and Hrodey (2019) observed biased re-entry of migrating sea lamprey into traps with a studded tile substrate, which supports the notion of CIDs influencing eel ladder interactions. All sea lamprey used in our study were previously captured in USFWS assessment traps and that may have selected for a sub-set of individuals by screening out sea lamprey that were more risk-averse or more active. A limitation of our study, therefore, is that using previously trapped sea lamprey may have introduced a bias that affected the outcome because the animals were exposed to risk (e.g. interacting with fishways and traps). We did not pre-test our experimental sea lamprey for CIDs in behaviour prior to inclusion in trials so it is not possible to evaluate this hypothesis more robustly here.

During the semelparous spawning migration lampreys may become less risk-prone because the cost of failing to detect and respond to threats (e.g. predators) at this stage cannot be offset (Luhring et al. 2016; but see Seebacher et al. 2013). This may, at least in part, account for both failed fish passage attempts for lampreys generally and low-success of trapping for sea lamprey

specifically, particularly where these engineered structures do not exceed the animal's physiological limits. Although attempts to navigate fishways and surmount weirs are energetically costly to lampreys during their migration - necessitating some recovery time (Quintella et al. 2004, 2009) - this alone is not a satisfactory explanation for the delays in passage observed at such structures, which may exceed two weeks (Almeida et al. 2002; Foulds and Lucas 2013; Tummers et al. 2016b; Castro-Santos et al. 2017; Goodman and Reid 2017; Pereira et al. 2017). In our study sea lamprey that did not ascend the ramp stopped moving earlier in the presence of alarm cue. Changes in activity levels by migratory sea lamprey in response to the alarm cue in natural streams appear highly context dependent, with increased (Hume et al. 2015) and decreased activity levels observed (Luhring et al. 2016) likely due to changes in internal state as sexual maturity proceeds.

The current study confined sea lamprey spatially (albeit in a large arena within a stream) and avoidance of risky behaviour in such circumstances (i.e. exposure on the ramp) may be a less costly response following threat detection compared to increased activity. Larval sea lamprey occupying burrows also reduce movement rates when exposed to alarm cue in mesocosms (Wagner et al. 2016). Delays caused by inefficient fishways may negatively impact spawning success of imperiled lamprey populations by disrupting its timing, which consists of several highly synchronized events (migration, spawning, and embryonic development) strongly dependent on stream temperatures (Johnson et al. 2015). Therefore, reducing barrier-induced delay by increasing the rate of encounter with fishway entrances, as well as improving fishway passage efficiency, is necessary. The sea lamprey alarm cue, when applied to a stream side opposite to a barrier-integrated trap, reduced the time taken to locate the entrance by ~50% (Hume et al. 2015), suggesting this cue has potential to reduce delays at barriers. Furthermore, if a fishway entrance is located on the opposite side of a stream from where alarm cue is applied then sea lamprey encountering the entrance will not have immediately reacted to the cue. Exposure to the cue may affect motivation to enter the fishway if it perceives itself to be at risk of predation, as suggested by lower entrance rates in its presence in this study. Instead, alarm cue applied opposite will act to aggregate sea lamprey near the entrance, increasing the probability of encounter and subsequent entrance (Bravener and McLaughlin 2013).

Upon reaching the ramp base, sea lamprey in this study were capable of ascending (n = 188/192, 97.9% total). These rates of transit are far in excess of those reported by Rooney et al. (2015) for anadromous sea lamprey ascending a 67-m wide, 1.4 m high sloping weir with a 2-m wide section of studded tiles (8%). Rooney et al. (2015) could not distinguish between sea lamprey passing the weir by using studded tiles, or via another route. Importantly, Rooney et al. (2015) conducted their study in a natural stream and sea lamprey were, therefore, not spatially constrained within a mesocosm. D'Aguiar (2011) found comparable, but lower, rates of transit (80%) using the same Milieu Inc. substrate on up to an 80° incline and constraining Great Lakes sea lamprey to a much smaller scale experimental apparatus. Both field and laboratory-based evaluations of studded plastic tiles have revealed very low efficiency for European river lamprey *Lampetra fluviatilis*, a species more similar in size to Great Lakes sea lamprey compared with the

anadromous form of sea lamprey. When vertically-mounted (i.e. with studs protruding laterally towards a false wall) within a baffled fishway (1.3 m head), passage rate was estimated at 7% (Tummers et al. 2016b) and only 20-27% (studs, Vowles et al. 2017) or 37% (bristle media, Kerr et al. 2015) in a controlled flume environment with a 0.34 m high weir. When mounted as they were in this study (i.e. horizontally with studs protruding upwards) though not over the full area of the sloping face, passage rates of European river lamprey over an experimental 0.34 m high weir were still only 22-44% (Vowles et al. 2017) and 26% for a 1.3 m weir over a six week study period (Tummers et al. 2018).

Water velocity and depth, the size and spacing of studs on substrate tiles, substrate presentation (horizontal or vertical, and incline), and extent of studded tiles (multiples of body length) are all likely to influence the gait of lampreys. This may explain significant variation in the efficiency of different designs examined so far (Figure 2; Table 2). When presented with fully submerged dual-density studded tiles mounted horizontally on a weir European river lamprey typically attempted to burst-swim over the top of studs, rather than move between them (Vowles et al. 2017). Thus, European river lamprey may have utilized a boundary layer of reduced velocity that forms above fully submerged studded substrates. The geometry of horizontally-mounted dual-density studded tiles (designed principally for elvers and "yellow" eel) in Vowles et al. (2017) creates narrower gaps compared to those employed in the present study, which may preclude lampreys from swimming through this studded design. But the gaps between these larger studs are still wider than the likely lateral displacement of the head (based on generalized kinematic anguilliform models) of lamprey used in Vowles et al. (2017) (Figure 2, Ic and IIc). The dual-density Barry & Escott design would therefore perhaps encourage burst-swimming between studs if water depth was lower than the height of studs, preventing lamprey going over the top (Figure 2, IVc). Furthermore, the diagonal gaps between the smaller studs (intended for elvers in the original design) in Vowles et al. (2017) preclude lamprey in that study from moving between them as they are narrower than the average width of lamprey used (Figure 2, Ic and IIc). Single-density Barry & Escott "lamprey tiles" with wider spacing (Tummers et al. 2016b; Tummers et al. 2018; Figure 2, IIb and IIIb) also permit burst-swimming between studs, but if water depth exceeds stud height (Figure 2, IVb) lamprey may opt to move above studs within the boundary layer. In these circumstances studded substrates are acting to reduce water velocity and are not necessarily taking advantage of any anguilliform-specific ability or behaviour.

In Tummers et al. (2018) lamprey were tasked with travelling > 16 body lengths, compared to < 5 and < 4 body lengths in Vowles et al. (2017) and the present study, respectively (Figure 2, Va, b and c; Table 2). Quintella et al. (2009) found that anadromous sea lamprey perform frequent short bursts of swimming when challenged with high flows, interspersed with periods of rest attached to the substrate (~67 s swimming and ~99 s resting). To pass more difficult stretches, these fish increase the number of burst-swim movements, but not their duration. The longer distances challenging European river lamprey to ascend the weir in Tummers et al. (2016b, 2018) may exhaust them, resulting in low overall efficiency of the design. However, no data is available

from those studies to indicate how many body lengths lamprey travelled before failing. In the current study we found multiple transit attempts were more likely if sea lamprey attached to the ramp, indicating there is a cost to burst-and-attach movement in terms of reduced efficiency. Burst-swim-attach movement is energetically costly for lampreys, becoming more costly with increasing distance and velocity (Keefer et al. 2010; Kirk et al. 2016). Furthermore, Pacific lamprey climbing a vertical 1.4 m barrier rested at a rate that correlated strongly with the number of bouts of upward movement (Kemp et al. 2009). These observations are consistent with the suggestion that movement rates and resting duration are associated (Kramer and McLaughlin 2001). Therefore, tasking lampreys with ascending shorter sections of studded substrates (e.g. 5 body lengths) interspersed with resting areas may result in higher efficiencies. In addition, constraining lampreys in a relatively small area clearly improves studded ramp efficiency even up to an 80° angle (D'Aguiar 2011; this study) compared to when lampreys are unconstrained in a stream. One design consideration to aid sea lamprey passage of barriers would be to install a series of short, studded ramps that extend from the stream; each culminating in a pool that lampreys cannot fall back from. A lamprey must attempt to ascend the next ramp section following recovery from previous exertion and efficiency of such a design likely correlates with the proportion that successfully ascended the first section. Similar designs, but without studded substrate, are in use for Pacific lamprey which are capable of passing 100% of lamprey over 8 – 9 m high barriers in < 1 hour by suctorial climbing (e.g. Moser et al. 2011), a locomotion mode not used by sea lamprey or European river lamprey.

Explicit consideration of the number of attempts made by individuals can reveal deeper insight into how fishways perform and potentially highlight circumstances that create difficulties (Castro-Santos 2004; Keefer et al. 2014; Vowles et al. 2017). In this study, 19.8% (n = 37) of sea lamprey that attempted to ascend the ramp made multiple attempts, but only 4 individuals tried and subsequently failed to ascend overall. This suggests sea lamprey were highly successful in overcoming the physical challenge presented by the ramp (water velocity, stud spacing and size, extent, incline). European river lamprey individuals made up to 30 attempts each to transit similar studded substrates, although they faced higher water velocities (Vowles et al. 2017; Table 2). The authors of that study posit lamprey have difficulty at the ramp crest and get washed back or turned around. In our design we provided a gradual declined ramp of 30° at the ramp crest, which provides a less severe transition zone, preventing sea lamprey from extending their bodies unsupported into open space. We conclude, as with Goodman and Reid (2017) for Pacific lamprey, that platforms aiding lamprey transit of an inclined surface should extend beyond corners to avoid this circumstance and permit attachments all the way past the crest.

Steep surfaces (inclined or vertical) encountered during migrations are a strong selective pressure acting on diadromous fishes. Many varied locomotor solutions have evolved in response to this challenge, including the use of pectoral fins to create intermittent axial undulations (Schoenfuss and Blob 2003) and using oral and pelvic suckers for attachment (Blob et al. 2006). Lampreys are unlike other climbing fishes because they lack pectoral and pelvic fins, the latter of which are frequently modified to aid other species to ascend steep inclines. Pacific lamprey for

example can climb even vertical wetted surfaces in air using a modified anguilliform swimming motion; attaching to the surface, contracting their body, then rapidly straightening while maintaining contact with the surface and "sliding" vertically (Reinhardt et al. 2008; Kemp et al. 2009). Unlike Pacific lamprey, sea lamprey are not considered to be capable of climbing vertical obstructions, an observation used to construct barriers to prevent their upstream movement in the Great Lakes (Hunn and Youngs 1980). Because rivers draining to the Pacific tend to be high gradient and dominated by large waterfalls (Griffiths 2018), it is likely anadromous lampreys in this region capable of surmounting such obstacles were selected for. Sea lamprey spawning in Atlantic river drainages face far less severe challenges when returning to freshwater because of lower relief and river gradients (Griffiths 2018), so likely vertical climbing behaviour has not evolved in this species. Stud geometry on the ramp in the present study reduced lateral space for sea lamprey attempting to ascend. In Pacific lamprey, climbing requires very wide body amplitudes as they force their body upwards (Kemp et al. 2009). However, stud spacing in our study was such that sea lamprey were capable of moving between them with a gait similar to the lateral undulation described for terrestrial snakes (Bennet et al. 1974; Jayne 1986), whereby lamprey exert lateral force against studs contacting the body at multiple locations (Supplementary video files). In the absence of lateral resistance, for example during terrestrial locomotion, anguilliform fishes exhibit very wide lateral excursions of both the head and the tail (e.g. American eel *Anguilla rostrata*) and forward progress is therefore significantly slower than in water. The same pattern holds true when anguilliform fishes experience increasingly shallow water; ropefish *Erpetoichthys calabaricus* immersed to 25-50% of their body depth exhibit a similar gait to American eels moving on land (Pace and Gibb 2011). Corniuk (2019) found a small (15%, to 0.1 body lengths) increase in lateral excursion of sea lampreys' bodies when swimming in very shallow water. Therefore, stud spacing and geometry, and water depth all likely interacted to facilitate lateral undulation in sea lamprey in the current study. In the absence of closely-spaced studs or water depths that submerged them, sea lamprey may be incapable of ascending a 45° incline, however D'Aguiar (2011) observed sea lamprey ascending Milieu Inc. substrate that received no flowing water. Our data suggest sea lamprey may exhibit a gait transition from burst-swimming to what we here term "undulatory climbing behaviour" when faced with narrow gaps representing a certain proportion of the body width (Figure 2; Table 2), permitting movement up relatively steep slopes for short distances. The non-alternating stud geometry of single-density studded tiles used for European lamprey passage in the study by Tummers et al. (2018) (Fig. 2) is also less likely to support undulatory climbing behaviour of lamprey than one with alternating stud geometry and similar spacing.

The installation or retrofitting of studded tiles is gaining popularity as a remediation tool to achieve higher rates of passage for anguilliform and other long-bodied fishes compared to conventional fishway designs (Verdon et al. 2003; Baker and Boubée 2006; Vowles et al. 2015). However, passage rates for threatened lampreys using these tiles remain mediocre (Kerr et al. 2015; Rooney et al. 2015; Tummers et al. 2016; Vowles et al. 2017). Furthermore, where sea lamprey have become invasive there is significant pressure to find a means of selectively removing

this species from mixed assemblages of desirable fishes to alleviate the need for pesticide applications and the impacts of control barriers on non-target species (Siefkes et al. 2013; Sorensen and Johnson 2016). Sea lamprey are an excellent case study for bridging problems on either side of the management coin; because they are both imperiled and invasive, advances in one area will likely aid the other (Hansen et al. 2016). Using a mesocosm approach we have shown a ramp bearing studded tiles is capable of attracting and permitting the ascent of an exceedingly high proportion of Great Lakes sea lamprey. This could provide an effective tool for selectively removing this pest from natural streams if the ramp discharges into a trap. When used for restoration, we suggest that improper size and spacing of studded tiles create burst-swim challenges that may in fact hinder the movement of lamprey species, but more work is required to better understand why. In addition, our study revealed aspects of motivation that affected sea lamprey climbing efficiency separate from movement capacity that is manipulated further by the application of an alarm cue. This is consistent with recent observations that lampreys express intraspecific variation in passage behaviour (Kemp et al. 2009; Kirk and Caudill 2017), and supports the need to move beyond viewing fishway interactions in purely engineering *vs* fish swimming performance terms (Castro-Santos et al. 2017; Goodman and Reid 2017; Silva et al. 2018). Differences in stud spacing and presentation are more likely to account for reported variance in the efficacy of studded tiles between studies (Figure 2; Table 2) because none challenged lampreys with water velocities that exceeded their maximum swimming speed (Quintella et al. 2009; Russon and Kemp 2011; Hoover and Murphy 2018). Given that studded tiles are intended to reduce water velocity, and support anguilliform locomotion between the studs, to aid movement through difficult-to-pass areas, it seems unlikely lampreys will be negatively affected by water velocity if appropriately designed stud arrangements are used. This is suggestive that additional factors influence lamprey ability and motivation to engage with engineered structures, which goes beyond swim-speed alone. Extending these findings from the mesocosm to field-testing, and translating results from Great Lakes sea lamprey to additional taxa, will require a directed and evidence-based scientific approach.

ACKNOWLEDGEMENTS

We thank staff of the U.S. Fish and Wildlife Service for provisioning sea lamprey for this study, and the U.S. Geological Survey Hammond Bay Biological Station for access to their facility throughout the study period. We also thank Dr Robert Lennox and two anonymous reviewers for their comments on an earlier draft. The findings and conclusions are those of the authors and do not necessarily represent the views of the U.S. Fish & Wildlife Service. Our thanks to N. Corniuk, Z. Kellogg, L. Hetzler, G. Molinari, and L. Kivari for their assistance in the field. This work was supported by funding from the Great Lakes Fishery Commission (2016_WAG_54049).

FIGURES & TABLES

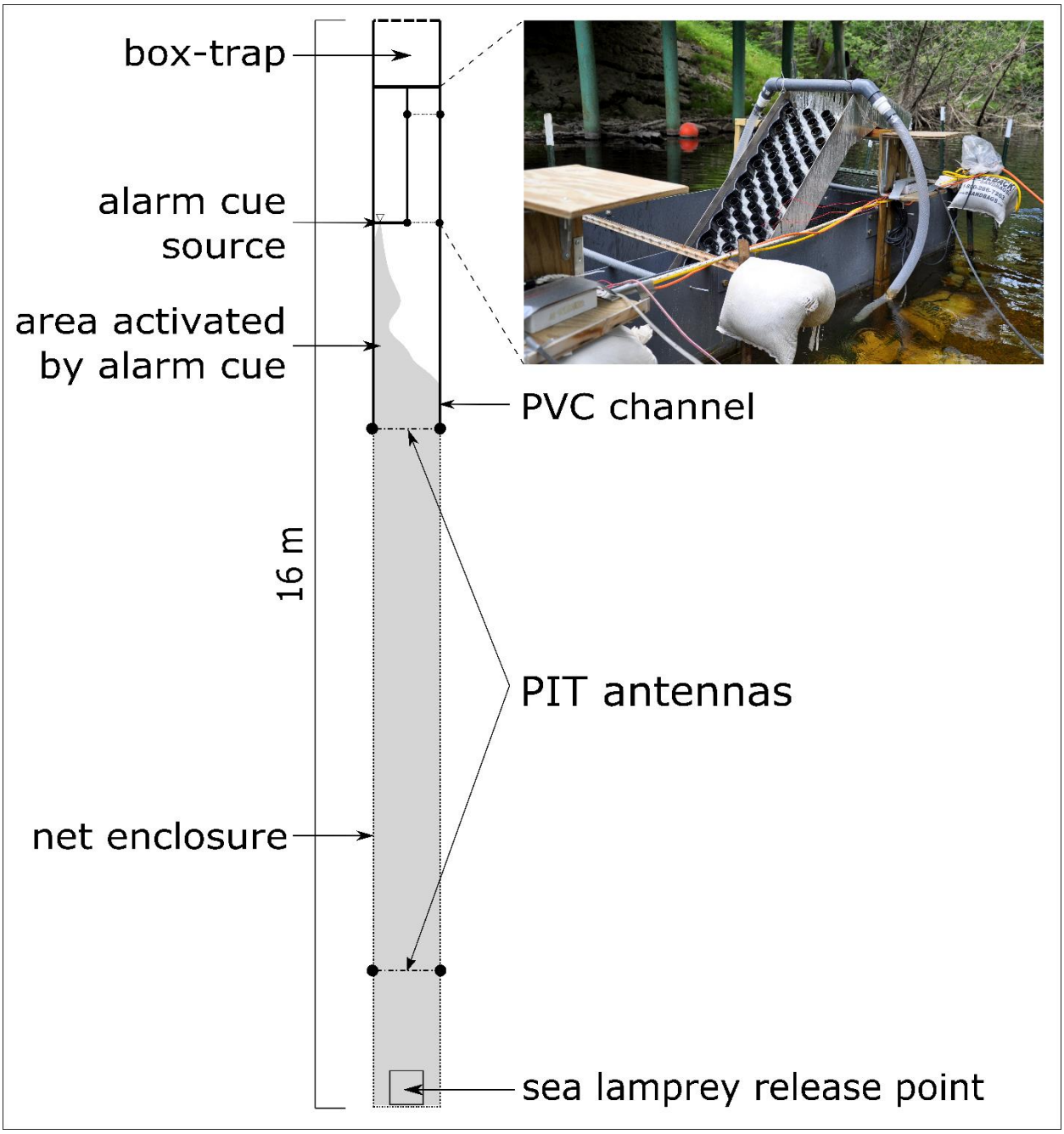
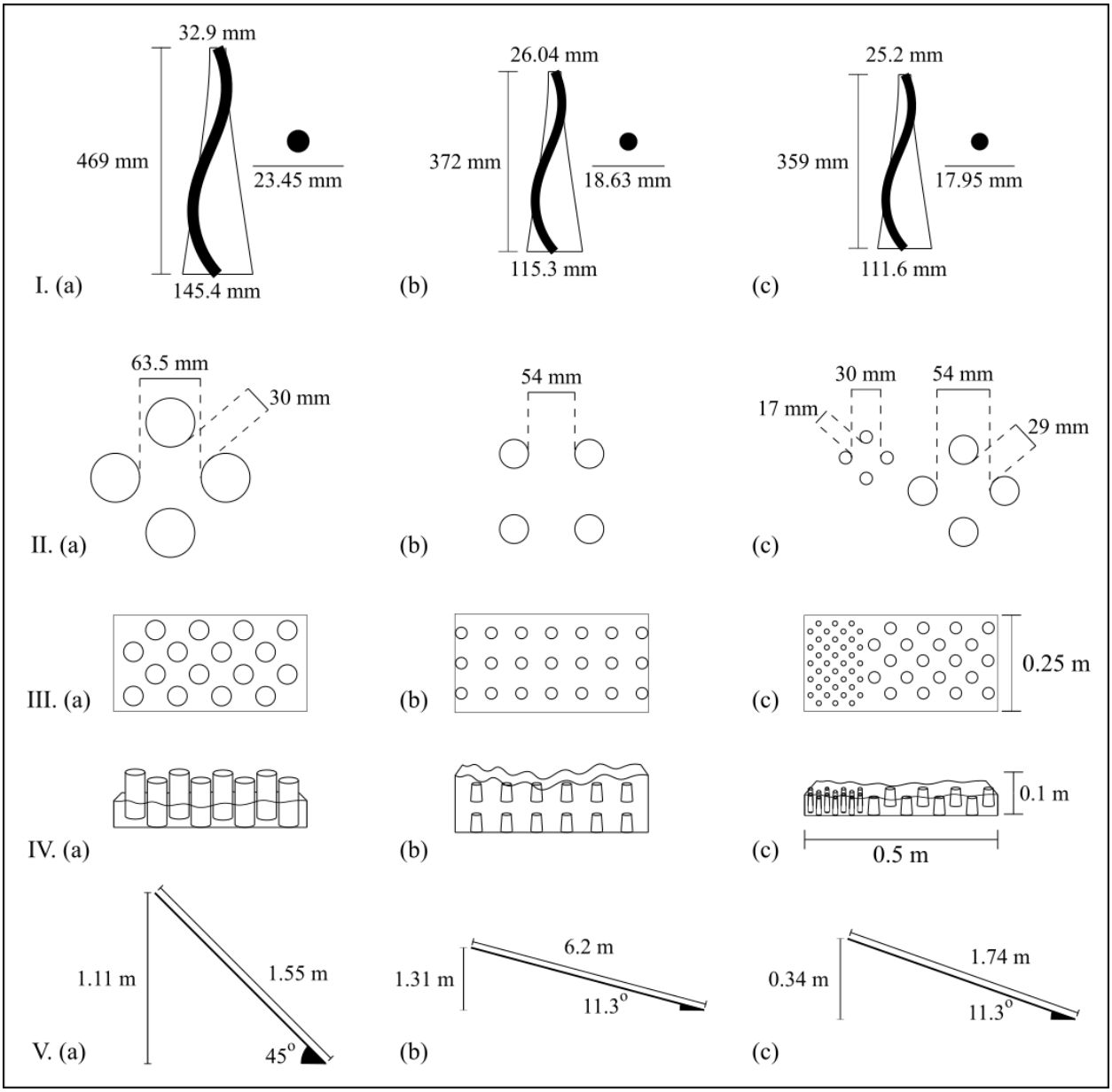
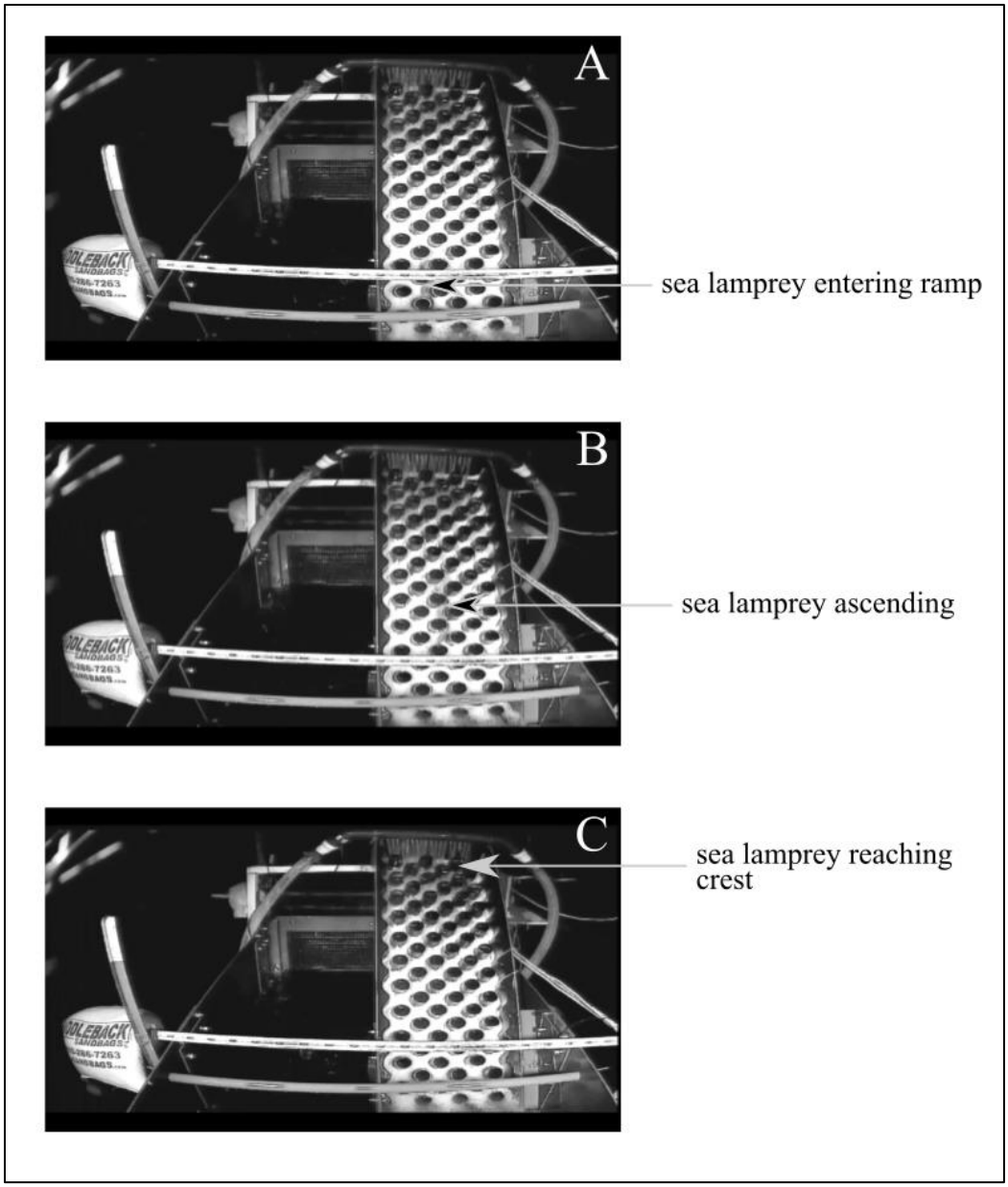


Figure 1. Schematic of the experimental apparatus. A 6 m long by 1 m wide PVC channel was preceeded downstream by a 10 m long by 1 m wide net enclosure, allowing sea lamprey to freely explore following their release from holding cages. Four PIT antennas (• · – · •) monitored movement of tagged sea lamprey. At the upstream extent of the mesocosm a ramp bearing Milieu Inc. studded plastic substrate was installed (photographic inset) adjacent to an area permitting flow from the stream. Alarm cue was present in 15/30 trials and the typical distribution of odor is represented by the shaded area.



543 Figure 2. Scale representations of study design components used in three studies testing lamprey
544 transit using studded plastic tiles mounted horizontally. Columns represent separate studies: a)
545 present study; b) Tummers et al. (2018); c) Vowles et al. (2017). Rows represent: I) generalized
546 lamprey body sizes based on mean total length and maximum lateral amplitude (estimated from
547 McClellan et al. 2016), and mean body diameters of lamprey used (a = Great Lakes sea lamprey,
548 b and c = European river lamprey); II) geometry and spacing of studs (a = Milieu Inc., b and c =
549 Barry & Escott Engineering); III) a single 0.25 x 0.5 m section of studded tile; IV) an isometric
550 view of III showing relative mean water depths in each study; V) schematic showing angle, extent,
551 and head height of each surface fitted with studded plastic substrate.



552

553 Figure 3. Sequence of sub-adult sea lamprey ascending the studded ramp. Sea lamprey begin
554 climbing at the water surface-ramp interface (A) before proceeding to move through the stud
555 arrangement (B) in either a straight bottom-to-top direction, or by moving diagonally to the edge
556 before ascending all the way to ramp crest (C) where they slid downward in to a trap on the other
557 side of the crest. Supplementary video files show this in real-time.

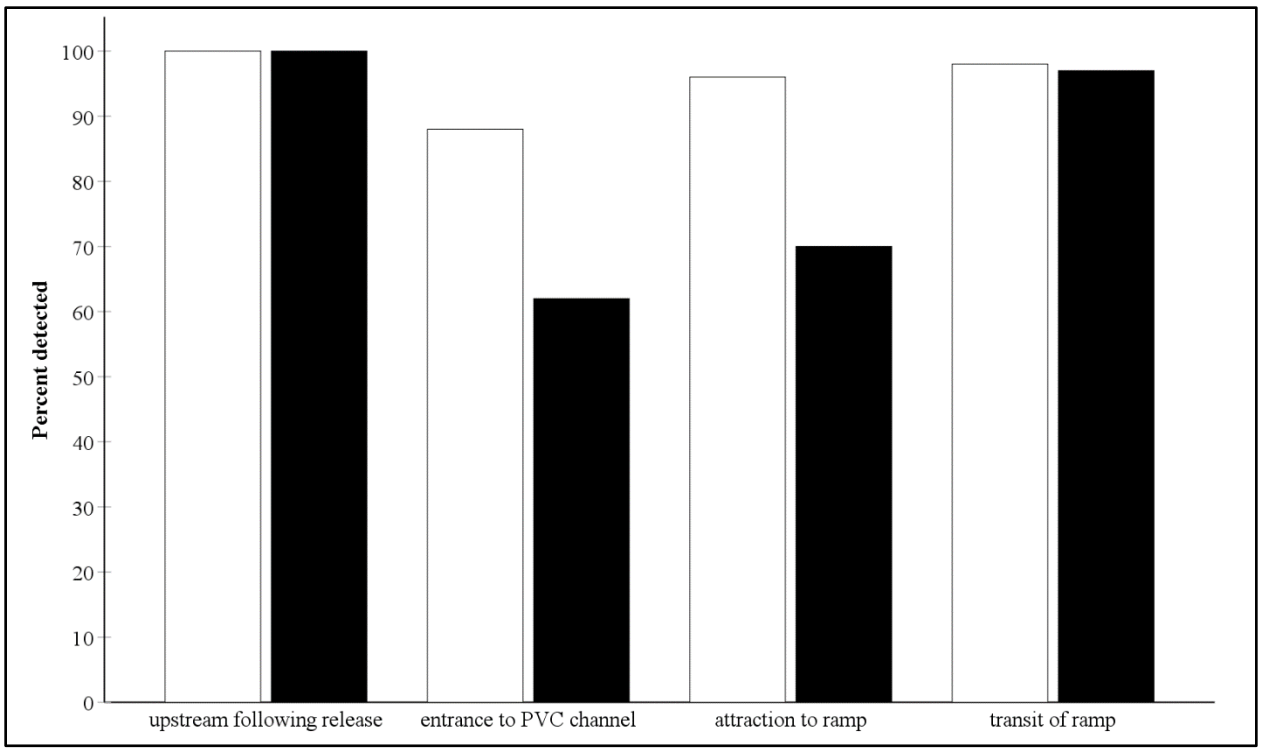
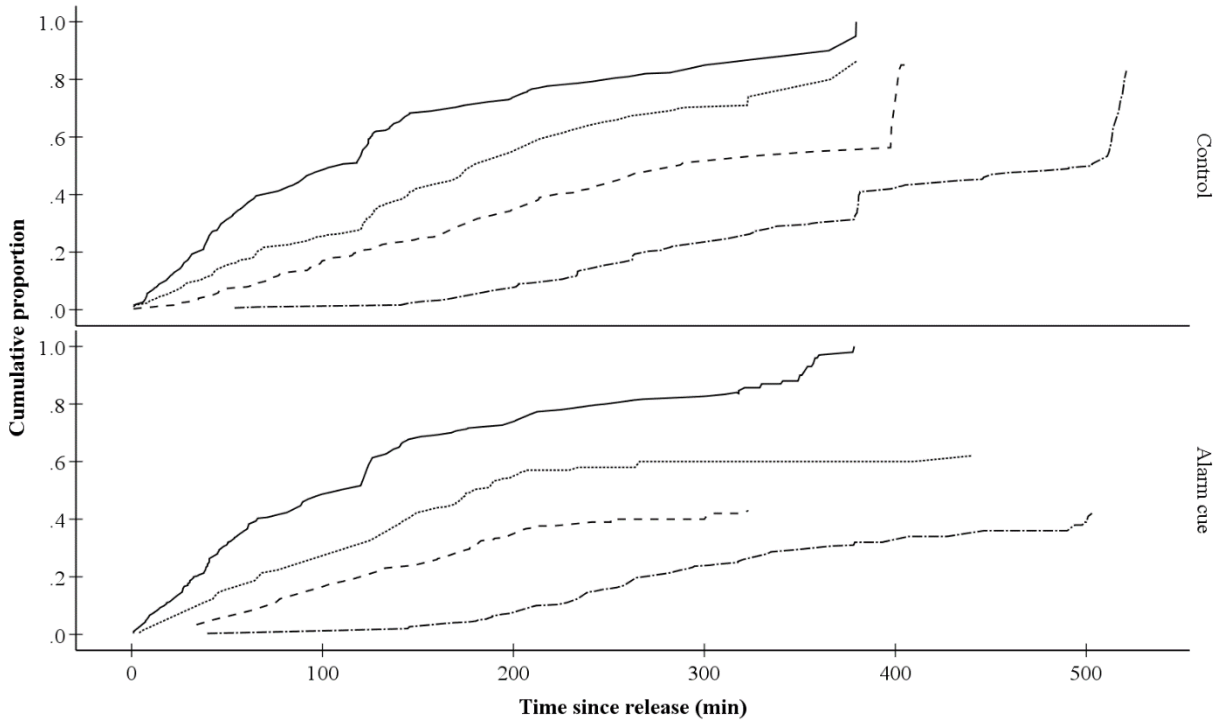


Figure 4. Percent of sea lamprey recorded at four PIT antennas within the mesocosm. Data shown are contingent on the number of available sea lamprey detected at each previous antenna. Data are treated separately for each treatment: control (white bars) or with alarm cue present (black bars). Although the presence of alarm cue reduced channel entrance and attraction to the ramp relative to control, transit efficiency was comparable between treatments.



564

565 Figure 5. Cumulative proportions of tagged sea lamprey detected (reading top to bottom): moving
566 upstream (solid line), entering PVC channel (dotted line), at the base of the ramp (dashed line),
567 and then transiting the ramp (dash-dot-dash line) as a function of time since release and separated
568 by treatment.

569 Table 1. Metrics used to evaluate Great Lakes sea lamprey *Petromyzon marinus* interaction with,
570 and performance of, a ramp provisioned with studded tiles to aid their transit upstream during
571 spawning migrations.

Metric Evaluated	Definition
Attraction efficiency	Number of sea lamprey detected at the base of the ramp as a percentage of those that entered the channel.
Transit efficiency	Number of sea lamprey that ascended the ramp and collected in the box trap as a percentage of those detected at the base of the ramp.
Number of transit attempts	A detection at the base of the ramp followed by ½ of the body length visible on the ramp surface in video footage.
Number of attachments	An attachment constitutes a stoppage of > 1 s on the ramp surface following initiation of a transit attempt.
Delay	Difference in time (min) between the first detection of an individual sea lamprey moving upstream following release and its last detection (either following transit of the ramp, or elsewhere in the arena).
Position at ramp entrance	The ramp surface was visually divided into three sections: left, center, and right, relative to facing upstream.

572 Table 2. Metrics derived from four studies testing lamprey transit using studded plastic tiles mounted horizontally and

Lamprey species	Head height (m)	Tile orientation[2]	Length of tiled section (BL)[3]	Incline(degrees)	Stud spacing (diagonal/horizontal; mm)[4]	Stud spacing relative to lamprey width (%)[5]	Water depth between studs (mm)	Water velocity within studded tiles (m s^{-1})	Attraction efficiency (%)	Passage efficiency (%)	Study
P. marinus[1]	1.11	horizontal	3.30	45	30/63.5	+22/+63	69 ± 17	0.2	85.3	97.9	this study
L. fluviatilis	0.34	horizontal	4.83	11.3	17/30 & 29/54	-6/+40 & +38/+67	55 ± 14	"low" [6]	n/a	44.4	Vowles et al. (2017)
L. fluviatilis	0.34	vertical	4.83	11.3	17/30 & 29/54	-6/+40 & +38/+67	55 ± 14	"low" [7]	n/a	27.3	Vowles et al. (2017)
L. fluviatilis	1.31	horizontal	16.67	11.3	83/54	+78/+66	150 +	n/a	43.5	25.6	Tummers et al. (2018)
L. fluviatilis	0.34	horizontal	4.83	11.3	17/30 & 29/54	-6/+40 & +38/+67	55 ± 14	"high" [8]	n/a	22.2	Vowles et al. (2017)
L. fluviatilis	0.34	vertical	4.83	11.3	17/30 & 29/54	-6/+40 & +38/+67	55 ± 14	"high" [9]	n/a	20	Vowles et al. (2017)
L. fluviatilis	1.31	vertical	31.11	11.3	83/54	+78/+67	500-550	n/a	85.8	7.1	Tummers et al. (2016b)

573 [1.] *Petromyzon marinus* refers to sea lamprey from the Laurentian Great Lakes basin. [2.] Orientation refers to how studded tile sections are mounted onto an inclined
574 surface, with horizontal being fixed flat (studs positioned perpendicular to surface, extending upwards into water column) and vertical being fixed along their
575 edge (studs positioned parallel to surface, extending towards a retaining wall). [3.] Body lengths (mm ± S.D.) = 469 ± 38.9 (this study); 359 ± 24 (Vowles et al.
576 2017); 372.5 ± 24.2 (Tummers et al. 2018); 360 ± 21 (Tummers et al. 2016b). [4.] Measured from the base of studs. [5.] Lamprey body widths estimated as 5% of
577 total body length. [6.] Max = 1.26 estimated on weir adjacent to tiles. [7.] Max = 2.03 estimated on weir adjacent to tiles. [8.] Max = 2.20 estimated on weir adjacent to
578 tiles. [9.] Max = 2.15 estimated on weir adjacent to tiles.

579 LITERATURE CITED

580 Aarestrup K, Lucas MC, Hansen JA (2003) Efficiency of a nature-like bypass channel for sea trout
581 (*Salmo trutta*) ascending a small Danish stream studied by PIT telemetry. Ecol Freshw Fish 12:
582 160-168.

583 Adams RD, Reinhardt UG (2008) Effects of texture on surface attachment of spawning-run sea
584 lampreys *Petromyzon marinus*: a quantitative analysis. J Fish Biol 73: 1464-1472.

585 Almeida PR, Quintella BR, Dias NM (2002) Movement of radio-tagged anadromous sea lamprey
586 during the spawning migration in the River Mondego (Portugal). Hydrobiologia 483: 1-8.

587 Baker CF, Boubée JAT (2006) Upstream passage of inanga *Galaxias maculatus* and redfin bullies
588 *Gobiomorphus huttoni* over artificial ramps. J Fish Biol 69: 668-681.

589 Bals JD, Wagner CM (2012) Behavioral responses of sea lamprey (*Petromyzon marinus*) to a
590 putative alarm cue derived from conspecific and heterospecific sources. Behavior 149: 901-923.

591 Beamish FWH (1974) Swimming performance of adult sea lamprey, *Petromyzon marinus*, in
592 relation to weight and temperature. Trans Am Fish Soc 103: 355-358.

593 Bennet S, McConnell T, Trubatch SL (1974) Quantitative analysis of the speed of snakes as a
594 function of peg spacing. J Exp Biol 60: 161-165.

595 Birnie-Gauvin K, Franklin P, Wilkes M, Aarestrup K (2018) Moving beyond fitting fish in to
596 equations: progressing the fish passage debate in the Anthropocene. Aquatic Conserv Mar Freshw
597 Ecosyst 2018: 1-11.

598 Blob RW, Rai R, Julius ML, Schoenfuss HL (2006) Functional diversity in extreme environments:
599 effects of locomotor style and substrate texture on the waterfall climbing performance of Hawaiian
600 gobiid fishes. J Zool (London) 268: 315-324.

601 Bunt, C.M., Castro-Santos, T., and Haro, A. (2012). Performance of fish passage structures at
602 upstream barriers to migration. River Res Appl 28: 457-478.

603 Byford GJ, Wagner CM, Hume JB, Moser ML (2016) Do native Pacific lamprey and invasive sea
604 lamprey share and alarm cue? Implications for use of a natural repellent to guide imperiled Pacific
605 lamprey in to fishways. N Am J Fish Manag 36: 1090-1096.

606 Castro-Santos T (2004) Quantifying the combined effects of attempt rate and swimming capacity
607 on passage through velocity barriers. Can J Fish Aquat Sci 61: 1602-1615.

608 Castro-Santos T, Haro A (2010) Fish guidance and passage at barriers. In: Domenci P, Kapoor BG
609 (eds.). Fish locomotion: an eco-ethological perspective (pp 62-89). Enfield, NH Science
610 Publishers.

611 Castro-Santos T, Shi X, Haro A (2017) Migratory behavior of adult sea lamprey and cumulative
612 passage performance through four fishways. Can J Fish Aquat Sci 74: 790-800.

613 Corniuk NL (2019) Modified Wetted Ramp Style Fishways as a Selective Fish Passage Device at
614 Low Crest Sea Lamprey Barriers in the Laurentian Great Lakes. E-Thesis, Eastern Michigan
615 University, Ypsilanti, Michigan USA.

616 D'Aguiar MJ (2011) The ability of sea lamprey (*Petromyzon marinus*) to utilize solid structural
617 components to climb inclined surfaces. Masters Thesis, University of Guelph.

618 Docker MF, Hume JB (2019) There and back again: lampreys in the 21st Century and beyond. In:
619 Lampreys: Biology, Conservation and Control Vol. 2. Springer Dordrecht pp 527-570.

620 Dodd HR, Hayes DB, Baylis JR, Carl LM, Goldstein JD, McLaughlin RL, Noakes DLG, Porto
621 LM, Jones ML (2003) Low-head sea lamprey barrier effects on stream habitat and fish
622 communities in the Great Lakes basin. J Great Lakes Res 29 (Supplement 1): 386-402.

623 Foulds WL, Lucas MC (2013) Extreme inefficiency of two conventional, technical fishways used
624 by European river lamprey (*Lampetra fluviatilis*). Ecol Eng 58: 423-433.

625 Frick KE, Corbett SC, Moser ML (2017) Climbing success of adult Pacific lamprey on a vertical
626 wetted wall. Fisheries Manag Ecol 24(3): 230-239.

627 Goodman DH, Reid SB (2017) Climbing above the competition: innovative approaches and
628 recommendations for improving Pacific lamprey passage at fishways. Ecol Eng 107: 224-232.

629 Gore JA (1996) Discharge methods and streamflow analysis. In: Hauer FR, Lambert G (eds)
630 Methods in stream ecology. Academic Press San Diego CA, pp 53-74.

631 Griffiths D (2018) Why does freshwater fish species richness differ between Pacific and Atlantic
632 drainages of the Americas? J Biogeogr 45: 784-792.

633 Grill G, Lehner B, Lumsdon AE, MacDonald GK, Zarfl C, Liermann CR (2015) An index-based
634 framework for assessing patterns and trends in river fragmentation and flow regulation by global
635 dams at multiple scales. Environ Res Lett 10: 015001.

636 Hansen MJ, Madenjian CP, Slade JW, Steeves TB, Almeida PR, Quintella BR (2016) Population
637 ecology of the sea lamprey (*Petromyzon marinus*) as an invasive species in the Laurentian Great
638 Lakes and an imperiled species in Europe. Rev Fish Biol Fish 26: 509-535.

639 Hoover JJ, Murphy CE (2018) Maximum swim speed of migrating sea lamprey (*Petromyzon*
640 *marinus*): reanalysis of data from a prior study. ERDC/TN ANSRP-18-1. Vicksburg MS: US Army
641 Engineer research and Development Center.

642 Hume JB, Meckley TD, Johnson NS, Luhring TM, Siefkes MJ, Wagner MC (2015) Application
643 of a putative alarm cue hastens the arrival of invasive sea lamprey (*Petromyzon marinus*) at a
644 trapping location. Can J Fish Aquat Sci 72: 1799-1806.

645 Hunn JB, Youngs WD (1980) Role of physical barriers in the control of sea lamprey (*Petromyzon*
646 *marinus*). Can J Fish Aquat Sci 37: 2218-2122.

647 Imre I, Brown GE, Bergstedt RA, McDonald R (2010) Use of chemosensory cues as repellents for
648 sea lamprey: potential directions for population management. J Great Lakes Res 36: 790-793.

649 Jayne BC (1986) Kinematics of terrestrial snake locomotion. Copeia 1986: 915-927.

650 Jellyman DJ (1977) Invasion of a New Zealand freshwater stream by glass-eels of two *Anguilla*
651 spp. New Zeal J Mar Fresh Res11: 193-209.

652 Johnson NS, Buchinger TJ, Li W (2015) Reproductive ecology of lampreys. In: Docker MF (ed)
653 Lampreys: biology, conservation and control. Springer Dordrecht pp. 265-303.

654 Keefer ML, Caudill CC, Moser ML (2014) Fishway bottleneck relief models: a case study using
655 radio-tagged Pacific lamprey. Trans Am Fish Soc 143: 1049-1060.

656 Keefer ML, Daigle WR, Peery CA, Pennington HT, Lee SR, Moser ML (2010) Testing adult
657 Pacific lamprey performance at structural challenges in fishways. N Am J Fish Manag 30: 376-
658 385.

659 Kemp PS (2016) Meta-analyses, metric and motivation: mixed messages in the fish passage
660 debate. River Res Appl 32: 2116-2124.

661 Kemp PS, Tsuzaki T, Moser ML (2009) Linking behaviour and performance: intermittent
662 locomotion in a climbing fish. J Zool 277: 171-178.

663 Kerr JR, Karageorgopoulos P, Kemp PS (2015) Efficacy of a side-mounted vertically oriented
664 bristle pass for improving upstream passage of European eel (*Anguilla anguilla*) and river lamprey
665 (*Lampetra fluviatilis*) at an experimental Crump weir. Ecol Eng 85: 121-131.

666 Kirk MA, Caudill CC (2017) Network analyses reveal intra- and interspecific differences in
667 behaviour when passing a complex migration obstacle. J Appl Ecol 54: 836-845.

668 Kirk MA, Caudill CC, Syms JC, Tonina D (2017) Context-dependent response to turbulence for
669 an anguilliform swimming fish, Pacific lamprey, during passage of an experimental vertical-slot
670 weir. Ecol Eng 106: 296-307.

671 Kirk MA, Caudill CC, Tonina D, Syms JC (2016) Effects of water velocity, turbulence and
672 obstacle length on the swimming capabilities of adult Pacific lamprey. Fisheries Manag Ecol 23:
673 356-366.

674 Klingler GL, Adams JV, Heinrich JW (2003) Passage of four teleost species prior to sea lamprey
675 (*Petromyzon marinus*) migration in eight tributaries of Lake Superior, 1954-1979. J Great Lakes
676 Res 29 (Supplement 1): 403-409.

677 Kramer DL, McLaughlin RL (2011) The behavioural ecology of intermittent locomotion. Am Zool
678 41: 137-153.

679 Laine A, Kamula R, Hooli J (1998) Fish and lamprey passage in a combined Denil and vertical
680 slot fishway. Fisheries Manag Ecol 5: 31-44.

681 Lavis DS, Hallett A, Koon EM, McAuley TC (2003) History of and advances in barriers as an
682 alternative method to suppress sea lampreys in the Great Lakes. J Great Lakes Res 29 (Supplement
683 1): 362-372.

684 Limburg KE, Waldman JR (2009) Dramatic declines in North Atlantic diadromous fishes.
685 BioScience 59: 955-965.

686 Lucas MC, Baras E (2001) Migration of freshwater fishes. Blackwell Science, Oxford, UK. pp
687 440.

688 Luhring TM, Meckley TD, Johnson NS, Siefkes MJ, Hume JB, Wagner MC (2016) A semelparous
689 fish continues upstream migration when exposed to alarm cue, but adjusts movement speed and
690 timing. Animal Behav 121: 41-51.

691 Lynch AJ, Cooke SJ, Deines AM, Bower SD, Bunnell DB, Cowx IG, Nguyen VM, Nohner J,
692 Phouthavong K, Riley B, Rogers MW, Taylor WW, Woelmer W, Youn SJ, Beard Jr TD (2016)
693 The social, economic, and environmental importance of inland fish and fisheries. Can J Fish Aquat
694 Sci 115-121.

695 Maitland PS, Renaud CB, Quintella BR, Close DA, Docker MF (2015) Conservation of native
696 lampreys. In: Docker MF (ed) Lampreys: biology, conservation and control vol. 1. Springer
697 Dordrecht pp 375-428.

698 McLaughlin RL, Hallett A, Pratt TC, O'Conner LM, McDonald GD (2007) Research to guide use
699 of barriers, traps, and fishways to control sea lamprey. J Great Lakes Res 33 (Special Issue 2): 7-
700 19.

701 McLaughlin RL, Marsden JE, Hayes DB (2003) Achieving the benefits of sea lamprey control
702 while minimizing the effects on nontarget species: conceptual synthesis and proposed policy. J
703 Great Lakes Res 29 (Supplement 1): 755-765.

704 McLean AR, McLaughlin RL (2018) Consistent individual differences in sea lamprey
705 (*Petromyzon marinus*) behaviour: implications for control via trapping. J Great Lakes Res 44: 482-
706 490.

McLeave JD (1980) Swimming performance of European eel ((*Anguilla anguilla* (L.)) elvers. J Fish Biol 16: 445-452.

Moser ML, Almeida PR, Kemp PS, Sorensen PW (2015) Lamprey spawning migration. In: Docker MF (ed) Lampreys: biology, conservation and control. Springer Dordrecht pp 215-263.

Nilsson C, Reidy CA, Dynesius M, Revenga C (2005) Fragmentation and flow regulation of the world's large river systems. Science 308: 405-408.

Pace CM, Gibb AC (2011) Locomotor behavior across an environmental transition in the ropefish, *Erpetoichthys calabaricus*. J Exp Biol 214: 530-537.

Pereira E, Quintella BR, Mateus CS, Alexandre CM, Belo AF, Telhado A, Quadrado MF, Almeida PR (2017) Performance of a vertical-slot fish pass for the sea lamprey *Petromyzon marinus* L. and habitat recolonization. River Res Appl 33: 16-26.

Poff NL, Hart DD (2002) How dams vary and why it matters for the emerging science of dam removal. BioScience 52: 659-668.

Poff NL, Zimmerman JKH (2010) Ecological responses to altered flow regimes: a literature review to inform the science and management of environmental flows. Freshwater Biol 55: 194-205.

Porto LM, McLaughlin RL, Noakes DLG (1999) Low-head barrier dams restrict the movement of fishes in two Lake Ontario streams. N Am J Fish Manag 19: 1028-1036.

Pratt TC, O'Connor LM, Hallett AJ, McLaughlin RL, Katapodis C, Hayes DB, Bergstedt RA (2009) Balancing aquatic habitat fragmentation and control of invasive species: enhancing selective fish passage at sea lamprey control barriers. Trans Am Fish Soc 138: 652-665.

Pringle C (2003) What is hydrologic connectivity and why is it ecologically important? Hydrol Process 17: 2685-2689.

Quintella BR, Andrade NO, Koed A, Almeida PR (2004) Behavioural patterns of sea lampreys' spawning migration through difficult passage areas, studied by electromyogram telemetry. J Fish Biol 65: 961-972.

Quintella BR, Póvoa I, Almeida PR (2009) Swimming behaviour of upriver migrating sea lamprey assessed by electromyogram telemetry. J Appl Ichthyol 25: 46-54.

Radinger J, Wolter C (2014) Patterns and predictors of fish dispersal in rivers. Fish Fish 15: 456-473.

Rahel FJ & McLaughlin RL (2018) Selective fragmentation and the management of fish movement across anthropogenic barriers. Ecol Appl 28: 2066-2081.

738 Reid SB, Goodman DH (2016) Free-swimming speeds and behavior in adult Pacific lamprey,
739 *Entosphenus tridentatus.* Environ Biol Fish 99: 969-974.

740 Reinhardt UG, Hrodey PJ (2019) Trap Happiness and Catch Bias in Sea Lamprey Traps. Fishes
741 4(34) doi:10.3390/fishes4020034.

742 Rooney SM, Wightman G, Ó'Conchúir R, King JJ (2015) Behaviour of sea lamprey (*Petromyzon*
743 *marinus* L.) at man-made obstacles during upriver spawning migration: use of telemetry to assess
744 efficacy of weir modifications for improved passage. Biol Environ Proc R Iri Acad 115: 125-136.

745 Russon IJ, Kemp PS (2011) Experimental quantification of the swimming performance and
746 behaviour of spawning run river lamprey *Lampetra fluviatilis* and European eel *Anguilla anguilla*.
747 J Fish Biol 78: 1965-1975.

748 Sanz-Ronda, F.J., Bravo-Cordoba, F.J., Fuentes-Perez, J.F., and Castro-Santos, T. (2016). Ascent
749 ability of brown trout, *Salmo trutta*, and two Iberian cyprinids – Iberian barbel, *Luciobarbus*
750 *bocagei*, and northern straight-mouth nase, *Pseudochondrostoma duriense* – in a vertical slot
751 fishway. Knowl Manag Aquat Ec 417: 1-10.

752 Seebacher F, Ward AJW, Wilson RS (2013) Increased aggression during pregnancy comes at a
753 higher metabolic cost. J Exp Biol 216: 771-776.

754 Schoenfuss HL, Blob RW (2003) Kinematics of waterfall climbing in Hawaiian freshwater fishes
755 (Gobiidae): vertical propulsion at the aquatic-terrestrial interface. J Zool (London) 261: 191-205.

756 Siefkes MJ, Steeves TB, Sullivan WP, Twohey MB, Li W (2013) Sea lamprey control: past,
757 present, and future. In: Taylor WW, Lynch AJ, Leonard NJ (eds) Great Lakes Fishery Policy and
758 Management: a binational perspective. Michigan State University Press, East Lansing pp. 651-
759 704.

760 Silva AT, Lucas MC, Castro-Santos T, Katopodis C, Baumgartner LJ, Thiem JD, Aarestrup K,
761 Pompeu PS, O'Brien GC, Braun DC, Burnett NJ, Zhu DZ, Fjeldstad H-P, Forseth T, Rajaratnam
762 N, Williams JG, Cooke SJ (2018) The future of fish passage science, engineering and practice.
763 Fish and Fish 19: 340-362.

764 Solomon DJ, Beach MH (2004) Fish pass design for eel and elver (*Anguilla anguilla)*. R&D
765 Technical Report W2-070/TR1 pp. 105.

766 Sorensen PW, Johnson NS (2016) Theory and application of semiochemicals in nuisance fish
767 control. J Chem Ecol 7: 698-715.

768 Tummers JS, Hudson S, Lucas MC (2016a) Evaluating the effectiveness of restoring longitudinal
769 connectivity for stream fish communities: towards a more holistic approach. Sci Total Environ
770 569-570: 850-860.

771 Tummers JS, Kerr JR, O'Brien P, Kemp P, Lucas MC (2018) Enhancing the upstream passage of
772 river lamprey at a microhydropower installation using horizontally-mounted studded tiles. Ecol
773 Eng 125: 87-97.

774 Tummers JS, Winter E, Silva S, O'Brien P, Jang M-H, Lucas MC (2016b) Evaluating the
775 effectiveness of a Larinier super active baffle fish pass for European river lamprey *Lampetra*
776 *fluviatilis* before and after modification with wall-mounted studded tiles. Ecol Eng 91: 183-194.

777 van Ginneken V, Antonissen E, Müller UK, Booms R, Eding E, Verreth J, van den Thillart G
778 (2005) Eel migration to the Sargasso: remarkably high swimming efficiency and low energy costs.
779 Journal of Experimental Biology 208: 1329-1335.

780 Verdon R, Desrochers D, Dumont P (2003) Recruitment of American eels in the Richelieu river
781 and Lake Champlain: provision of upstream passage as a regional-scale solution to a large-scale
782 problem. In: Dixon DA (ed) Biology, management, and protection of catadromous eels. Am Fish
783 Soc Symp 33 pp. 125-138.

784 Vowles AS, Don AM, Karageorgopoulos P, Kemp PS (2017) Passage of European eel and river
785 lamprey at a model weir provisioned with studded tiles. J Ecohydraulics 2: 88-98.

786 Vowles AS, Don AM, Karageorgopoulos P, Worthington TA, Kemp PS (2015) Efficiency of a
787 dual density studded fish pass designed to mitigate for impeded upstream passage of juvenile
788 European eels (*Anguilla anguilla*) at a model crump weir. Fisheries Manag Ecol 22: 307-316.

789 Wagner CM, Kierczynski KE, Hume JB, Luhring TM (2016) Exposure to a putative alarm cue
790 reduces downstream drift in larval sea lamprey *Petromyzon marinus* in the laboratory. J Fish Biol
791 89: 1897-1904.

792 Wagner CM, Stroud EM, Meckley TD (2011) A deathly odor suggests a new sustainable tool for
793 controlling a costly invasive species. Can J Fish Aquat Sci 68: 1157-1160.

794 Watz J, Nilsson PA, Degerman E, Tamario C, Calles O (2019) Climbing the ladder: an evaluation
795 of three different anguillid ell climbing substrata and placement of upstream passage solutions at
796 migration barriers. Anim Conserv doi:10.1111/acv.12485.